PROC. BIOL. SOC. WASH.
95(3), 1982, pp. 602–609

MORPHOLOGY AND DEVELOPMENT OF PLANKTONIC *LOLLIGUNCULA BREVIS* (CEPHALOPODA: MYOPSIDA)

Michael Vecchione

Abstract.—Planktonic *Lolliguncula brevis* can be identified by chromatophore patterns. The most consistent character in specimens <15 mm dorsal mantle length (DML) is a cluster of three dark (''red'') chromatophores posterior to the eyeball on the ventral surface of the head. The ventral surfaces of the mantle and cephalic appendages are covered with numerous red chromatophores. On all dorsal surfaces, such chromatophores are absent in small specimens (<3 mm DML) and sparse in larger specimens.

The genus *Lolliguncula* is unique among cephalopods in its ability to tolerate low-salinity waters (Brakoniecki 1980). The thumbstall squid, *Lolliguncula brevis* (Blainville 1823), is a common inshore species in the Gulf of Mexico (Hixon *et al.* 1980) and along western Atlantic coasts from Delaware (Haefner 1964, Whitaker 1980) to the Rio de la Plata (Voss 1956). The ecology of specimens large enough to be collected in otter trawls has been investigated (Gunter 1950, Dragovich and Kelly 1963, 1967, Hendrix 1979, Hixon 1980). The early life history of this species, however, is virtually unknown.

While investigating the community ecology of planktonic molluscs in the Middle Atlantic Bight (Vecchione 1979), I found inshore loliginid specimens with chromatophore patterns unlike those of the other common loliginid, *Loligo pealei.* I speculated that these specimens were *L. brevis* based on their distribution and the suggestions of Hall (1970) and Hunter and Simon (1975) that chromatophore patterns could be used to separate species of young loliginids. Shortly thereafter, McConathy *et al.* (1980) demonstrated species-specific differences in chromatophore patterns among hatchling loliginids with known parentage. They suggested that chromatophore pattern differences combined with potential morphometric differences could be used for taxonomic differentiation of young squids collected in the field.

Squids are very difficult to rear (Yang *et al.* 1980). Therefore, the only practical means of describing their development is by assembling a growth series from field collections. I present in this report a description of the post-hatchling development of *L. brevis* in the planktonic size range (<15 mm dorsal mantle length, DML) based on specimens thus collected.

Materials and Methods

The specimens reported here have been assembled from several zooplankton surveys. Details of collecting methods are available elsewhere (Grant 1979, Grant and Olney 1979, Meyer 1981, Vecchione *et al.* 1982). A total of 241 specimens (size range 1.4–40.0 mm DML) were collected in ~2000 plankton tows with 153–505 μm mesh nets. Gear types used included bongo frames, neuston frames, pull sleds, pushnets, and half-meter nets. All specimens were preserved in 2–4% form-

Table 1.—Specimens examined.

Region	No. of specimens	Dorsal mantle length Min.	$\bar{x}$	S.D.	Max.
Chesapeake Bay	15	1.7	4.0	5.6	23.0
Virginia shelf	49	1.8	3.6	5.5	40.0
Calcasieu estuary	27	1.6	2.5	0.6	4.1
Louisiana shelf	150	1.4	2.2	1.4	13.7

aldehyde in seawater buffered with sodium borate. Areas sampled included a major estuary and the continental shelf of the southern Middle Atlantic Bight and a large estuary and the continental shelf in the northwestern Gulf of Mexico (Table 1).

All specimens were examined and measured under a dark-field dissecting microscope with ocular micrometer. Morphometric measurements were the same as those of Vecchione (1981). Measurements were to the nearest 0.02 mm but have been rounded to 0.1 mm because I lack confidence in the precision of measurement of nonrigid structures to 10^{-2} mm.

I paid particular attention to chromatophore placement. McConathy *et al.* (1980) divided chromatophores into two categories: "reds" and "yellows." I have followed this classification and terminology. The chromatophores were usually expanded on the preserved specimens analyzed in this study. This contrasted with the typical condition of contracted chromatophores in live specimens as described by McConathy *et al.* (1980). Expanded red and yellow chromatophores overlapped considerably. The latter were very lightly pigmented (perhaps because of bleaching by the preservative), making it difficult to distinguish the positions of all yellow chromatophores. I have therefore based the descriptions herein primarily on the red chromatophores. The figures were drawn with expanded red chromatophores as the planktologist would normally see them in preserved spec-

Table 2.—Morphometrics of specimens from one Middle Atlantic Bight sample. DML, dorsal mantle length; MW, mantle width; HL, head length; HW, head width; FL, fin length; WAF, width across fins; AL, length of third pair of arms; TL, tentacle length.

Specimen	DML	MW	HL	HW	FL	WAF	AL	TL
1	8.9	4.4	3.0	4.1	2.6	5.4	3.0	4.4
2	7.3	3.5	2.7	3.2	1.7	3.6	2.5	3.4
3	4.4	2.2	2.2	2.2	1.0	2.5	1.1	1.9
4	2.6	1.7	1.3	1.5	0.4	1.2	0.8	0.9
5	2.9	1.7	1.5	1.6	0.5	1.5	0.7	1.1
6	2.7	1.5	1.4	1.5	0.5	1.4	0.3	0.8
7	3.2	1.9	1.5	1.7	0.7	1.6	0.8	1.1
8	3.8	2.3	1.8	2.0	0.7	1.8	1.0	1.7
9	2.0	1.3	1.1	1.1	0.4	0.9	0.3	0.8
10	2.7	2.0	1.6	1.7	0.5	1.3	0.7	1.2
11	2.6	1.7	1.4	1.4	0.5	1.5	0.7	1.1
12	4.1	2.1	1.9	2.1	1.0	2.0	1.0	2.0
13	3.3	1.8	1.7	1.7	0.6	1.8	0.8	1.3
14	3.2	1.7	1.6	1.7	0.4	1.4	0.6	0.9

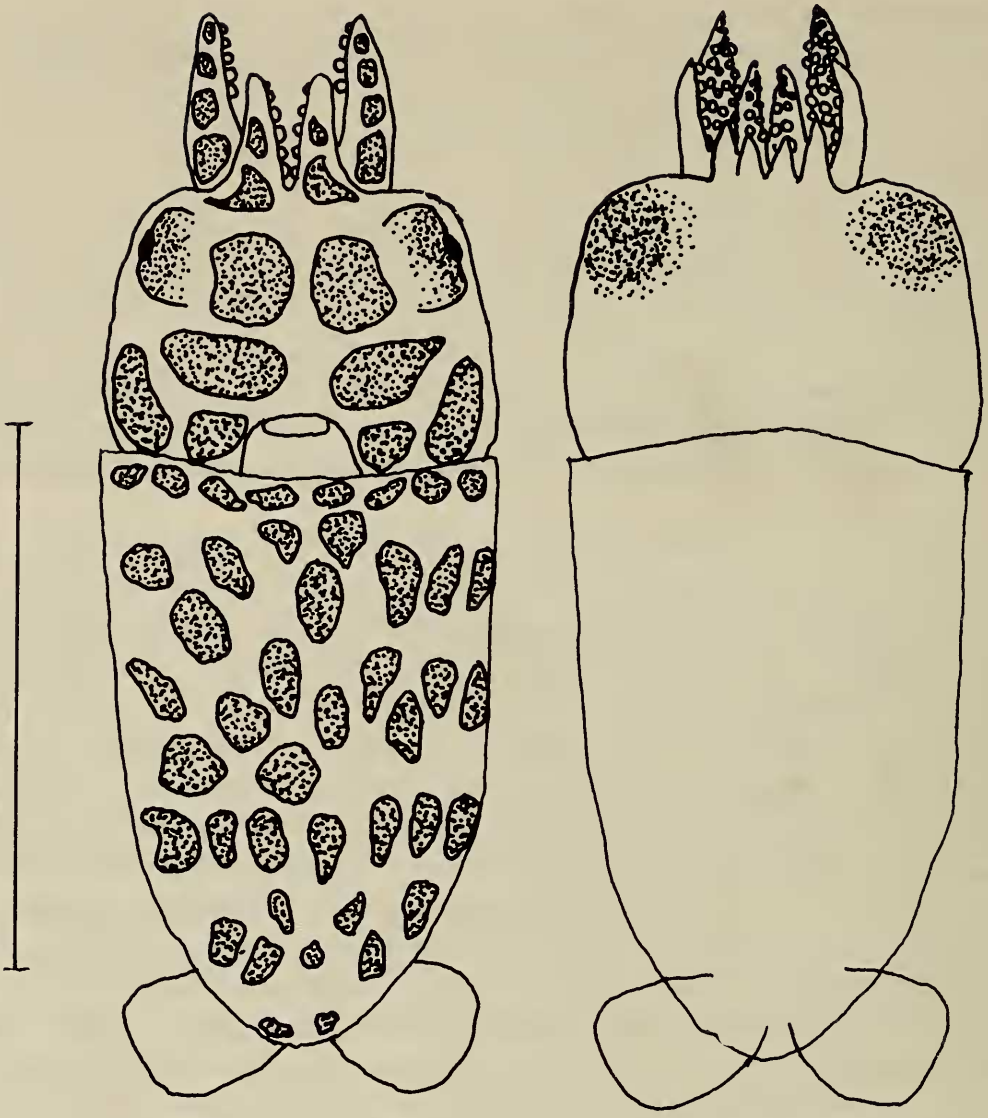

Fig. 1. *Lolliguncula brevis* (DML = 2.3 mm) showing placement of red chromatophores; left, ventral view; right, dorsal view. Scale line = 2 mm.

imens. Because few specimens were >4.5 mm DML and because many specimens of all sizes appeared damaged during collection or preservation, the following descriptions were based on specimens which were arbitrarily selected based on state of preservation within representative size ranges.

Identification and Development

The smallest specimens considered in this study closely matched the description by McConathy *et al.* (1980) of *L. brevis* hatchlings. For example, a 2.3 mm DML specimen (Fig. 1) lacked dorsal red chromatophores on either the head or the mantle. On the ventral surface of the head posterior to each eyeball, a triangular cluster of 3 red chromatophores matched that described for *L. brevis*. The number of red chromatophores on the ventral mantle surface (43) was within the range for hatchling *L. brevis* (36–44) but well above those of *Loligo pealei* and *L. plei* (15–32). Mantle chromatophores, however, were not arranged in the 7 transverse rows described in *L. brevis* by McConathy *et al.* (1980). Red chro-

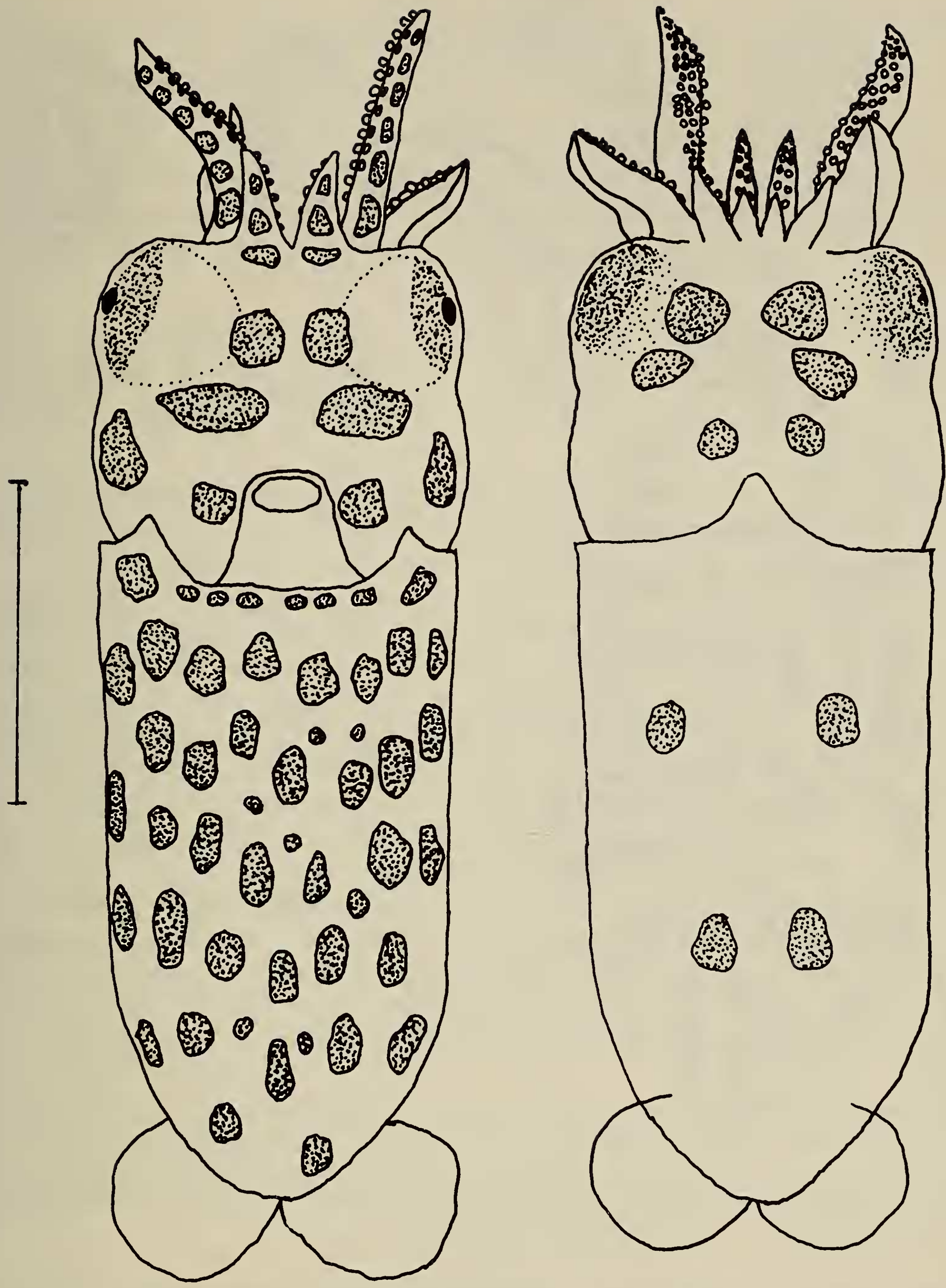

Fig. 2. *Lolliguncula brevis* (DML = 4.5 mm) showing placement of red chromatophores; left, ventral view; right, dorsal view. Scale line = 2 mm.

matophores on the cephalic appendages were confined to the ventral surfaces of the tentacles and fourth pair of arms. Yellow chromatophores were discernable on this specimen at the approximate locations described by McConathy *et al.* (1980).

A 4.5 mm DML specimen of *L. brevis,* representative of the 3.5–5.5 mm DML size range, had red dorsal chromatophores, 4 on the mantle and 6 on the head

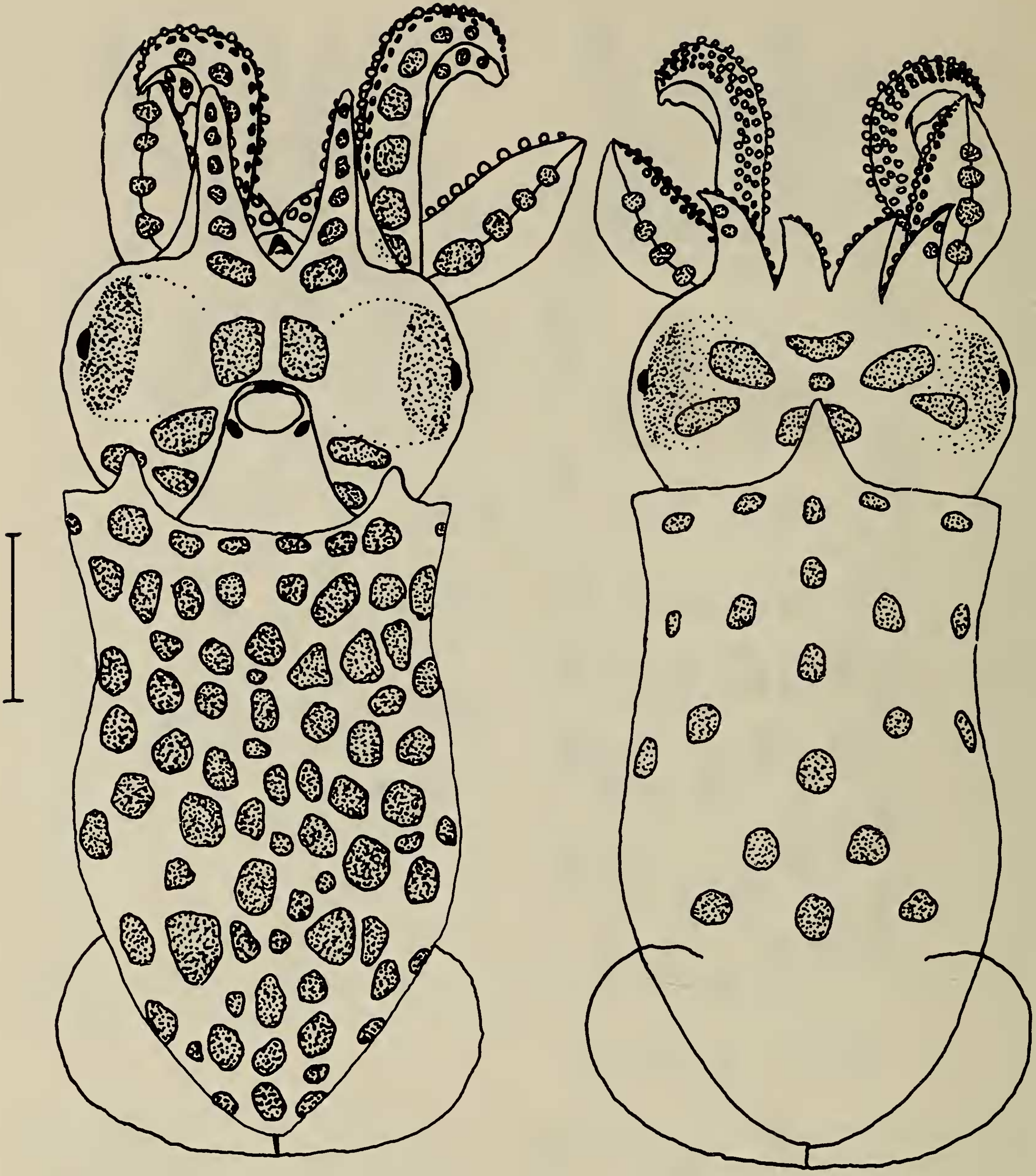

Fig. 3. *Lolliguncula brevis* (DML = 9.7 mm) showing placement of red chromatophores; left, ventral view; right, dorsal view. Scale line = 2 mm.

(Fig. 2). I have not yet found any specimens with only 2 red chromatophores on the dorsal mantle. I therefore cannot state the size at which these features first develop. Ventral placement of red chromatophores was similar to that of smaller specimens, including triangular clusters posterior to the eyeballs and numerous chromatophores (50) on the ventral mantle. Chromatophores had been added to the ventral rows on the tentacles and fourth arms. A second row of very dark chromatophores had also been added to the tentacles at the bases of the ventral suckers. This row was present in all specimens >4.5 mm DML but absent in smaller specimens. At 4.5 mm DML the third pair of arms had developed a swimming margin. The fins remained separated at the posterior mantle extremity. Three pronounced anterior mantle lobes were present in this specimen, one dorsal and 2 ventrolateral. Similar but smaller lobes were seen in a 3.8 mm DML specimen but were absent in smaller specimens.

Variability in chromatophore development was apparent in 2 specimens of 6.6 mm DML and one of 7.1 mm DML. All of these specimens were similar in overall morphology to the 4.5 mm DML specimen described above. Numbers of mantle chromatophores varied, however, as follows:

DML	dorsal-mantle chrom.	ventral-mantle chrom.
6.6	12	52
6.6	15	47
7.1	9	48

In a 7.4 mm DML specimen the fins were joined just posterior to the mantle end. This specimen had 14 dorsal- and 51 ventral-mantle chromatophores.

The specimen in Fig. 3 measured 9.7 mm DML. Gross morphology included large anterior dorsal and ventrolateral mantle lobes, fins joined posterior to the mantle end, and comparatively large eyeballs. Triangular clusters of red chromatophores were located ventroposterior to the eyeballs. A third row of chromatophores on the tentacles was located on the recently developed swimming margins. The swimming margins on the third pair of arms had developed a row of chromatophores. Red chromatophores on the mantle included 21 dorsal and 75 ventral. The dorsal surface of the head contained 8 red chromatophores and the second pair of arms each had 2 red dorsal chromatophores.

A 13.7 mm specimen was similar in appearance to the juvenile *L. brevis* commonly taken in otter trawls. There were 33 dorsal and 98 ventral red chromatophores on the mantle. The number of chromatophores indicated rapid increase of chromatophores in this size range. The dorsal surface of the fins, which were joined posterior to the mantle, had numerous small red chromatophores along the posterior edge as well as small yellow chromatophores scattered over the entire dorsal surface.

A limited set of morphometric observations on specimens 2.0–8.9 mm DML from a single sample (Table 2) were not significantly different from similar observations on *Loligo pealei* described by Vecchione (1981).

Discussion and Conclusions

Morphometric indices are not suitable for separating the young of the two common genera of inshore squids. However, given fresh specimens it should be possible to separate *L. brevis* from *L. pealei* and *L. plei* using differences in the ratio of dorsal : ventral red mantle chromatophores at a given size. This character, though, is increasingly variable in larger (>5 mm DML) specimens.

The size-frequency distribution of planktonic specimens was strongly skewed toward small sizes. These small individuals (<4 mm DML) were identifiable by use of the chromatophore criteria of McConathy *et al.* (1980). Most lacked red dorsal chromatophores and all had high numbers of red chromatophores on the ventral surface of the mantle. These ventral chromatophores were not, however, organized into 7 distinct transverse rows as described by McConathy *et al.* (1980).

Figures of late-stage embryos of *L. brevis* by Hall (1970) and Hunter and Simon (1975) show chromatophore patterns which do not match those presented here. I agree, however, with McConathy *et al.* (1980:279) that "Because the primary interest of these studies was either morphological or embryological and not specifically about chromatophores, the chromatophore arrangements depicted may be inexact."

Chromatophores on the mantle are subject to abrasion in net-captured specimens. Head chromatophores seem to be more protected, perhaps because the head can be partly withdrawn into the mantle. Of the specimens examined for this study, all but one had 3, rather than 4, red chromatophores posterior to the eyeballs on the ventral surface of the head. The one exception appeared to have been damaged as it had 3 uniform-sized chromatophores on one side and 2 similar-sized and 2 small (fragments?) chromatophores on the other side. This triangular cluster is a very consistent character suitable for generic identification of planktonic specimens, contrasting with the condition in *L. pealei* and *L. plei* of a trapezoidal arrangement of 4 red chromatophores (McConathy *et al.* 1980; Vecchione, pers. obs.).

Acknowledgments

It is a pleasure to acknowledge the assistance of Cathy Meyer and Don Weston, whose comments improved an earlier draft of this paper, and of Deanne Bonvillain, who typed the manuscript. Comments by an anonymous reviewer were very helpful in finalizing the manuscript. Contribution No. 1071 of the Virginia Institute of Marine Science.

Literature Cited

Brakoniecki, T. F. 1980. *Lolliguncula tydeus,* a new species of squid (Cephalopoda; Myopsida) from the Pacific coast of Central America.—Bulletin of Marine Science 30:424–430.

Dragovich, A., and J. A. Kelly. 1963. A biological study and some economic aspects of squid in Tampa Bay, Florida. Pp 87–102 *in* Gulf and Caribbean Fisheries Institute, Proceedings of the 15th Annual Session.

———, and ———. 1967. Occurrence of the squid, *Lolliguncula brevis* in some coastal waters of western Florida.—Bulletin of Marine Science 17:840–844.

Grant, G. C. 1979. Middle Atlantic Bight zooplankton: Second year results and a discussion of the two-year BLM-VIMS survey.—Virginia Institute of Marine Science Special Report in Applied Marine Science and Ocean Engineering 192, 236 pp.

———, and J. E. Olney. 1979. Lower Bay zooplankton monitoring program: An introduction to the program and results of the initial survey of March 1978.—Virginia Institute of Marine Science Special Scientific Report 93, 92 pp.

Gunter, G. 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including commercial shrimp.—Publications of The Institute of Marine Science 1:7–51.

Haefner, P. A. 1964. Morphometry of the common Atlantic squid, *Loligo Pealei,* and the brief squid, *Lolliguncula Brevis* in Delaware Bay.—Chesapeake Science 5:138–144.

Hall, J. R. 1970. Description of egg capsules and embryos of the squid, *Lolliguncula brevis,* from Tampa Bay, Florida.—Bulletin of Marine Science 20:762–768.

Hendrix, J. P. 1979. Osmotic concentration changes in the bay squid *Lolliguncula brevis* (Blainville, 1823) at various salinities.—Bulletin of the American Malacological Union 1979:69–70.

Hixon, R. F. 1980. Growth, reproductive biology, distribution and abundance of three loliginid squid species (Myopsida, Cephalopoda) in the Northwest Gulf of Mexico.—Ph.D. dissertation, University of Miami, 92 pp.

———, R. T. Hanlon, S. M. Gillespie, and W. L. Griffin. 1980. Squid fishery in Texas: Biological, economic, and market considerations.—Marine Fisheries Review 42:44–50.

Hunter, V. D., and J. L. Simon. 1975. Post-cleavage morphology in the squid *Lolliguncula brevis* (Blainville, 1823).—Veliger 18:44–51.

McConathy, D. A., R. T. Hanlon, and R. F. Hixon. 1980. Chromatophore arrangements of hatchling loliginid squids (Cephalopoda, Myopsida).—Malacologia 19:279–288.

Meyer, C. E. 1982. Zooplankton communities in Chesapeake Bay seagrass systems.—M.S. Thesis, College of William and Mary, 88 pp.

Vecchione, M. 1979. Planktonic molluscan faunal structure across a large scale environmental gradient.—Ph.D. dissertation, College of William and Mary, 153 pp.

———. 1981. Aspects of the early life history of *Loligo pealei*. Journal of Shellfish Research 1:171–180.

———, C. E. Meyer, and C. L. Stubblefield. 1982. Zooplankton. Chapter 8 *in* Final Report on Contract DE-AC-96-80P010228 with the U.S. Department of Energy. McNeese State University, Lake Charles, Louisiana. 69 pp.

Voss, G. L. 1956. A review of the cephalopods of the Gulf of Mexico.—Bulletin of Marine Science of the Gulf and Caribbean 6:85–178.

Whitaker, J. D. 1980. Squid catches resulting from trawl surveys off the southeastern United States.—Marine Fisheries Review 42:39–43.

Yang, Y. T., R. T. Hanlon, R. F. Hixon, and W. H. Hulet. 1980. First success in rearing hatchlings of the squid *Loligo pealei* Lesueur 1821.—Malacological Review 13:79–80.

Research and Development, McNeese State University, Lake Charles, Louisiana 70609.